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Insect eyes are constructed so that much of the destruction of irrelevant data and pre-processing of vital information is accomplished by the receptor array itself, reducing substantially the computational load placed on the neural system.

One of the most important mechanisms for destruction of irrelevant data is coarse spatial sampling. At long range, spectral properties of objects then become particularly important as a source of signals conveying specific information about qualities of those objects.

Colored wing patterns of butterflies provide important signals for recognition of species and sex, but little is known about butterfly color vision. This study analyzes data from

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optophysiological measurements of intact butterfly eyes. It demonstrates great diversity in absorbance spectra of visual pigments and spectral sensitivity functions of photoreceptors, and characterizes quantitatively those functions. Reflectance spectra of wing patches are measured microspectrophotometrically. Calculated quantum catches for photoreceptors viewing illuminated wing patches indicate which wing features have value as signals.

Some butterflies have red markings that are not detectable by most insects, but themselves possess specialized red-shifted receptors that are well stimulated by those red markings. The tetrachromatic Apodemia mormo enjoys the widest visible spectrum and greatest far-red sensitivity of any terrestrial animal.

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INSECT COMPOUND EYES:
DESIGN OF PHOTORECEPTOR ARRAYS FOR IMAGE PRE-PROCESSING

FINAL REPORT

GARY D. BERNARD

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III. BODY OF REPORT

A. STATEMENT OF THE PROBLEM STUDIED

Successful insect species have developed strategies for finding and acquiring food, detecting and avoiding predators, navigating, finding refuge, selecting a proper mate, and locating a suitable site for egg-laying. Several sensory modes are used to accomplish these tasks, but for many species vision is crucially important. Visually specialized insects are interesting subjects for study because of the diversity in the optical and physiological properties of their compound eyes, driven by evolutionary adaptation to the diversity of specialized behaviors and lifestyles.

Compared to vertebrates, insects are very small. How is it that such tiny eyes can be effective in meeting their visual needs? The sheer quantity of visual data impinging upon an eye is immense. The visual system must destroy most of that data, yet extract and process a small subset which contains information vital to the species. The problem seems to be a severe one.

Should the optics and photodetector array acquire as much data as possible, then rely on the neural system to sift the relevant from the irrelevant? No. Insects have a much more successful strategy. Their eyes are constructed so that much of the destruction of irrelevant data and pre-processing of real information is accomplished by the receptor array itself. This reduces substantially the computational load placed on the neural system.

One of the most important mechanisms for destruction of irrelevant data is coarse spatial sampling. Spatial resolution of insect eyes is seldom better than one cycle/degree, about 100 times worse that of a human eye (rev: Wehner[1]). Thus, spatial detail becomes important for an insect only at short range (< ten body-lengths). At long range, spectral and temporal properties of objects become particularly important as a source of signals conveying specific information about qualities of those objects. Color vision is, therefore, a particularly important mechanism fully developed by some insects.

Of all insect groups, the butterflies are best suited to studies of color vision. They make most extensive use of chromatic signals in mating, food-finding, and oviposition behaviors. Butterfly natural history and genetics are among the best known of all insect groups.

Butterfly color vision is mediated by a photoreceptor array that contains from three to five distinct spectral types of receptor. My noninvasive physiological and photochemical studies of the last decade have revealed great interspecific diversity in the spectral properties of visual pigments and photoreceptors of butterflies. This project selects representative visually specialized butterfly species, characterizes quantitatively the spectral properties of their photoreceptors, and compares the spectral design of the receptors to the spectral properties of wings and host plants. The overall goal is to understand the

principles according to which the spectral properties of receptor arrays are selected.

B. BACKGROUND

Visually Mediated Behavior of Butterflies

Butterflies lead very specialized lives. For example, it is common for the caterpillars of a butterfly species to accept only one species of foodplant. Thus, gravid females must reliably locate the proper foodplant. Vision is known to be important for hostplant detection, particularly at long range.

Courtship and mating must occur, of course, before eggs can be laid. Males engage in visual searches for females, looking for females with wings that have the proper color contrasts, size, and type of wing movement (reviewed by Wehner[1]; Silberglied[2]). At long range, the wing shape is not at all important, nor is the fine structure of color patterns. Presence of bands or stripes of expected color against expected background, however, may be very important. Ultraviolet (UV) components have been shown to be important in particular cases.

Spectral Sensitivity

Compound eyes of insects (reviews: Goldsmith & Bernard[3]; Autrum[4]; Bernard[5]) spatially sample through an array of lenses packed closely on the curved surface of the head. Underlying each lens is a cylindrical group of 8-12 photoreceptor cells that are heterogeneous in their spectral, spatial, and polarizational properties. Each receptor cell contains a long, thin rhabdomere that absorbs light owing to the presence of membrane-bound visual pigment. The primary event that leads to vision is the photochemical change in a visual pigment molecule that is caused by absorption of a photon.

Wavelength affects the probability that the photon will be absorbed by visual pigment. After a visual pigment molecule absorbs a photon and is isomerized, however, all information about the wavelength of that photon is lost. Thus, spectral analysis must be accomplished by groups of receptors that have two or more distinct spectral sensitivity functions (rev.: Wyszecki & Stiles[6]; Cornsweet[7]).

Following psychophysical notation, I define the **S-receptor** as the type with peak sensitivity at shortest wavelength, the **M-receptor** as the type with peak at intermediate wavelength, and the **L-receptor** as the type with peak sensitivity at long wavelength.

Extent of Visible Spectrum

The visible spectrum for humans extends from 400nm (deep violet) to 700nm (deep red). Insects, on the other hand, are known to see in the near-ultraviolet down to wavelengths as short as 300nm. Prior to the late 1970's it was held that butterflies were blind for wavelengths greater than about 620nm, while birds were blind for wavelengths less than about 400nm. Thus, it was

thought that red/orange patches are visual signals for birds but not butterflies, while violet or UV markings are signals for butterflies but not birds. It is now known that both statements are much too simplistic. Some butterfly species have special long-wavelength photoreceptors that allow them to see even further into the red than humans (Bernard[8]). On the other hand, some bird species have special receptors that allow them to see in the near-UV (Chen et al[9]). The behavioral, ecological, and evolutionary consequences of these two important findings are not yet understood.

Intracellular Optical Physiology

Photoreceptor cells of most insects contain intracellular pigment granules that move in response to illumination of the cell's photodetector organelle, the rhabdomere. In the dark-adapted state, these granules are dispersed throughout the cytoplasm of the receptor cell. If the cell is well illuminated, the granules move centripetally, congregating next to the rhabdomere where they are illuminated by the evanescent boundary layer of light guided by the rhabdom waveguide. Absorption, reflection, and scattering by the granules decrease the transmittance of the rhabdom, causing a loss in sensitivity of the receptor cell. This is called the **pupillary response** (Stavenga[10]).

Pigment migration within a cell is mediated exclusively by photoisomerization of visual pigment contained within that cell's rhabdomere. Thus, the granules in a cell can be used as an intracellular probe of the physiological response of that cell. Most insects have fused rhabdoms containing several spectral types of receptor, so the generalized pupillary response contains contributions from all receptor types.

Pupillary sensitization (Bernard[11]), however, makes it possible to isolate responses from only one receptor type and measure its spectral sensitivity function over most of the visible spectrum. The trick is to design the spectral content and intensity of the constant measuring beam so that it partially light-adapts the pupil of the desired spectral type, but leaves the pupils of all other spectral types dark-adapted. Pupillary responses from the light-adapted pupil are considerably faster than those from dark-adapted pupils because the distance the granules must move to exert an optical effect is smaller. Thus, the sensitivity of a moderately light-adapted pupil to short flashes is much greater than the sensitivity of dark-adapted pupils. This approach has been used to record from S-, M-, and L-receptors of bumblebees (Bernard & Stavenga[12]), honeybees (Bernard & Wehner[13]; Wehner & Bernard[14]), moths (Bernard et al[15]), and from specialized red-sensitive L-receptors of butterflies (Bernard[8]).

This non-invasive method (Bernard[16]), "Intracellular Optical Physiology", has the distinct advantages that: a) the animal under study is completely intact and healthy with undisturbed optics, retinal morphology, and physiology; b) responses are

stable and reproducible over very long periods of time -- as long as five months in individuals of some butterfly species; c) the eye region that contributes to the response can be precisely localized and bounded; and, d) both physiological and photochemical measurements can be performed on the same receptor cells.

Retinal Densitometry, Photochemistry, and Dark-Processes

Eyeshine caused by tapetal reflectors makes the intact butterfly eye an excellent preparation for spectroscopic study of visual pigments. Consider the optics: The visual pigments are contained within a long, thin rhabdom waveguide that is terminated optically by a reflector. This spectroscopic sample of photopigment is illuminated efficiently by a pair of lenses[17]. The lens-waveguide-reflector unit is wrapped in shielding pigment, protecting it from stray light. Performance of this system is unmatched. The level of stray light is about 0.05% and two-way photochemical changes of more than density 2.0 have been measured (Bernard[18]).

Like other insects, butterfly visual pigment is converted by light to a photoproduct ("metarhodopsin") that has a different absorption spectrum than the native form of the visual pigment. Measurements of difference spectra can be analyzed to determine the absorption spectra of both forms. Unlike other insects, butterfly metarhodopsin decays rapidly from the rhabdom in the dark. After discovering this fact, I exploited it to bleach visual pigment from the rhabdom and to measure directly the absorption spectrum of butterfly visual pigment (Bernard[19]). Prior to my work on butterflies it was thought that insect metarhodopsins were necessarily stable in the dark and that bleaching of insect visual pigments was therefore impossible (Langer et al[20]).

The kinetics of metarhodopsin's decay and visual pigment's regeneration depend strongly on temperature (Bernard[18,21]). This property, coupled with the fact that bleaching is possible in butterflies, is very important for this project. It enables quantitative measurement of both the absorbance spectrum and overall density of each spectral type of visual pigment. Those results, together with the optically measured spectral sensitivity functions, enable very high-quality, quantitative characterization of the spectral properties of the photoreceptor array.

Optical Stimulation of a Receptor

The optical stimulation (quantum catch) of a receptor is Q, the number of photons absorbed per unit time by the receptor's visual pigment[7,22].

$$Q = \int Q_o(\lambda)\, R(\lambda)\, S(\lambda)\, d\lambda$$

where $Q_0(\lambda)$ is the quantum flux of daylight illumination[6],
$R(\lambda)$ is the wing's reflectance spectrum, and
$S(\lambda)$ is the spectral sensitivity function for the photoreceptor cell.

Since the neural system can process only the information provided by the receptor cells, computations of stimulus values are a useful means of characterizing the neural image at the level of the receptor cells. The receptor potential is a saturating, hyperbolic function[22] of Q.

C. APPROACH TO THE PROBLEM

Between 1973 and 1985 I acquired data from many species and had qualitative evidence for diversity of color vision systems, but had not published because of ambiguities of possible interpretations of the experimental spectra. My ancient DEC LAB-8/E computer limited severely the scope of experiments and allowed only rudimentary analysis.

The proposal for this three-year project, started in 1/86, included replacing the lab-computer system and installing a powerful workstation computer for scientific data analysis. This provided the tools necessary for accurate, quantitative characterization of the spectral properties of butterfly photoreceptor systems and those of the colored objects known to be important for species survival -- wings and hostplants. The overall goal is to understand the principles according to which the spectral properties of receptor arrays are selected.

Specific goals of this three-year research project were to:

a) measure the spectral properties of each receptor type, including both physiological measurements of the spectral sensitivity function and photochemical measurements of visual-pigment absorption spectrum, in the same photoreceptor cells.

b) develop analytical methods to compare quantitatively to absorbance nomogram-template functions derived from visual pigments of vertebrate rods and cones; extend the presently available templates to include the beta band as well as the long wavelength, log-linear tail of the alpha band.

c) Document the extent of the diversity of butterfly color-vision systems, particularly the ability to see at long wavelengths (in the orange - red spectral region). Pay particular attention to closely related species that have very different wing coloration and/or very different receptor sets.

d) Measure the reflectance spectra of colored wing patches, then characterize neural images at the level of the receptor axons by computing the relative optical stimulation (quantum catches) for each spectral type of receptor viewing each daylight-illuminated patch.

The original proposal included a section on polarization vision. Reviewers of the proposal recommended that I drop that section and concentrate on the more interesting topic of color vision. I did so.

D. SUMMARY OF THE MOST IMPORTANT RESULTS

1. Analysis of Absorbance Spectra of Visual Pigments

Because my methods produce high quality absorbance and sensitivity spectra over a very wide spectral range (340nm - 700nm), proper analysis of mixed responses requires accurate knowledge of the spectrum of a single receptor type, including both the beta band and the log-linear tail. Published nomogram templates are inadequate because they are limited to the neighborhood of the alpha peak, and predict neither the short-wavelength beta band nor the long-wavelength, log-linear tail of the absorbance spectrum (MacNichol[23]).

I created improved templates for absorbance as a function of normalized frequency-ratio, for both rod and cone visual pigments, by incorporating the best spectrophotometric data and modern electrophysiological data (Bernard[24]). Eighth-order polynomial approximations are very accurate. See Figure 1.

My experimental absorption spectra for butterfly visual pigments were fit very well by the vertebrate-cone template, even including the beta band. Figure 2A shows a least-squares fit of the cone absorbance-template to a partial bleach of the L-receptors of Brassolis. This absorbance spectrum is typical of P530 visual pigments found in the L-receptors of many insects including bees[12,13] and moths[15], as well as some other butterflies[8,18].

Figure 2 indicates the great diversity among butterfly species in the spectral properties of L-receptor visual-pigments. P510 of the buckeye (Fig. 2B) represents the short-wavelength limit for butterfly L-receptors. Note that absorption is negligible for wavelengths > 600nm. Many butterflies such as heliconiids, pierids, danaids, and lycaenids have a visual pigment with lambda-max in the range 550nm - 560nm. An example, P555 of the western checkerspot is shown in Fig. 2C; this pigment absorbs well in the orange-red (600nm-650nm) spectral band.

The long-wavelength limit for the lambda-max of vertebrate, retinal-based visual pigments is about 580nm[26]; Figure 2D shows that the Copper butterfly, Lycaena nivalis, possesses P574, close to that limit. This visual pigment is more sensitive at long wavelengths than the red-sensitive P565 visual pigment of the human red-sensitive cone.

2. Analysis of Pupillary Action Spectra

Even though the generalized pupillary response of butterflies may contain contributions from several spectral types of receptor, it is possible to manipulate substantially the summation rules for the mixed response through: i) pupillary sensitization to short flashes, ii) bleaching, or iii) use of very long, dim flashes.

Very tight least-squares fits of theoretical absorptance spectra to short-flash spectral sensitivity functions show that only a single receptor type contributes. Figure 3A shows a least-squares fit of absorptance[25] (calculated from the cone absorbance-template) to the short-flash spectral sensitivity function measured from the very same receptor cells of Brassolis

from which the absorbance spectrum Fig. 2A was obtained. The precision of the fit to the cone function is excellent, even as far down on the long-wavelength tail as -3.5 log-units. A similar function based on the rod polynomial, which has a shallower tail than the cone polynomial, fits poorly. Thus, absorption spectra of butterfly visual pigments are essentially identical to those of vertebrate cone visual pigments.

Figure 3B shows the short-flash, pupillary sensitivity function from L-receptors of the Buckeye, which is well fit by a P511(+-1) absorptance function. This is consistent with the 510nm(+-1) estimate for the pigment absorbance function (Fig. 2B).

Long-flash spectra obtained by eliciting small responses from multiple receptor types are well fit by a linearly weighted sum of sensitivity functions of the contributing receptor types[25]. Together with photochemical measurements, this provides strong evidence for presence of minority receptor-types and a means for characterizing their properties. An example for a western Checkerspot E. chalcedona is shown in Fig. 3C.

In absence of photochemical data this would be a difficult spectrum to interpret because of the strange shape of the broad secondary peak. However, Fig. 2C shows that this eye contains visual pigment P556. The good fit of sensitivity functions R355 and R556 to the pupillary action spectrum of Fig. 3C, in the range 350-580nm, is strong evidence for presence of S-receptors R355. What about the poor fit for wavelengths > 580nm? One possible interpretation is, an artefact of stray-light leakage through reddish shielding pigment. Another possibility is, increased sensitivity owing to the presence of a minority, red-sensitive photoreceptor.

The latter possibility is probably correct, as shown in a similar experiment with the closely related eastern Checkerspot E. phaeton. This butterfly possesses P560, but the sensitivity function of its L-receptors (Fig. 3D) departs dramatically at short wavelengths from the absorptance spectrum expected for P560. In this eye the L-receptors are filtered by a photostable, blue-absorbing, red-transmitting filter. A precedent for this optical principle was first established in Sulphur butterflies by Ribi[27].

3. Results for M-Receptors

Properties of M-receptors (receptors having peak sensitivity at intermediate wavelengths) can be studied after bleaching the visual pigment of L-receptors. An example is shown in Figs. 4A-B for the Florida Viceroy, whose L-receptors contain an unusual visual pigment P515 (close relatives posses P530). After bleaching P515, the long-flash pupillary action spectrum (Fig. 4B) is dominated by S-receptor R350 and M-receptor R450. Photochemical measurements (not shown) support the hypothesis that M-receptors of the Viceroy contain visual pigment P450.

Similar experiments with the Sulphurs of genus Eurema (Fig. 4D) show that their M-receptors contain visual pigment P424, a substantial spectral shift compared to P450 of the Viceroy.

4. Two New Classes of Butterfly Visual Pigment

My early work on red-sensitivity in butterflies[8] indicated that the Metalmark Apodemia mormo possesses greater sensitivity in the far-red than any known insect. A new round of experiments with both sexes of this butterfly was very productive:

a) Results enabled accurate determination of the absorbance spectrum of this far-red visual pigment (Fig. 5A), revealing an alpha band with peak at 600nm having a shape identical to that of an A1-based visual pigment of vertebrate cones. It was even possible to measure the beta band of P600. Very poor fits to A_2 absorption spectra indicate that the chromophore of P600 is not 3-dehydroretinal, but is probably 3-hydroxyretinal. This P600 has a lambda-max that is at least 20nm greater than any known retinal-based visual pigment.

b) Rhabdoms in the frontal region of the male eye contain density > 0.5 of visual pigment P600, in photoreceptor cells that lack a pupillary response!

c) This presented a golden opportunity to follow in-vivo photoconversion of P600 to its photoproduct M508, using pure far-red light of wavelengths 700nm - 720nm. Results prove that P600 is not simply a conventional visual pigment filtered by blue/green-absorbing photostable pigment as describe above for Checkerspot butterflies (Figs. 4C-D), but is a pure, unshielded visual pigment that has a lambda-max of 600nm, and correspondingly high sensitivity in the far red (Fig. 5A).

d) The eye of the female is not the same as the male, containing less than half of the male's titer of P600, but in cells that DO exhibit a pupillary response.

e) Action spectra at long wavelengths are very different in the two halves of the female eye. The upper half (Fig. 5B, yellow beam) was dominated by a new class of receptor, having peak sensitivity at 505nm. This very clear isolation of receptor R505 was a surprise; There was no hint from the photochemical studies that visual pigment P505 was present, which is strong evidence that the photochemistry of P505 involves no spectral shift following photoisomerization. Switching from yellow to white measuring beams caused substantial increase in pupillary sensitivity at short wavelengths, owing to contributions from sensitized receptors R340 and R450.

f) Pupillary sensitivity of the lower half of the female eye (Fig. 5C) at long wavelengths is dominated by P600. Photochemical measurements supported the conclusion that P600 is present only in the ventral half of the eye.

g) In collaboration with J.K. Douglass and T.H. Goldsmith of the Yale Biology Department, we measured action spectra of the electroretinogram (ERG) of the male eye, which showed that P600 is indeed a visual pigment, contained in receptor cells that contribute to the ERG. Analysis of ERG action-spectra confirmed the presence of P505 and P600, and revealed the presence of two additional spectral classes of receptor, R340 and R450. Thus, the butterfly Apodemia mormo is tetrachromatic (R340, R450, R505, and R600), and is a Guiness Book candidate for the widest visible

spectrum and greatest far-red sensitivity of any terrestrial animal, and the greatest lambda-max of any retinal-based visual pigment.

h) Both wing surfaces of both sexes contain iridescent scales that reflect far-red light that is not visible to most invertebrates but is visible to P600 of Apodemia. These scales may have value as signals for species recognition.

5. Detectability of Red Wing Colors

One possibility for the (Darwinian) adaptive significance of the diversity of butterfly color-vision systems is to maximize the detectability of spectral signals flown by wings and host plants. A widely accepted conclusion among entomologists is that insects, including butterflies, "can't see red" because sensitivity of the typical invertebrate L-receptor R530 to monochromatic red (approx. 650nm) is below 1% of that at 530nm. Results presented above show that some butterfly species have high sensitivity at 650nm. However, reflectance spectra from wing colors are broadband, not narrowband. How bright is a red wing-patch, and how great is its contrast against the background when viewed by an L-receptor? Consider the following example:

The nymphalid butterfly Anartia amathea has wings with white spots and red bars on a dark-brown background. Reflectance spectra for white, red, and brown patches are shown in Fig. 6A. Reflectance of the red bars is very low for wavelengths less than 550nm, rising to a peak at 700nm. Behavioral experiments indicate that the red markings are important signals for mating behavior[28]. Compare quantum catches for specialized red-sensitive L-receptors of a male Anartia amathea (Bernard[8]), to those for the typical invertebrate R530 L-receptor of another nymphalid species, Vanessa cardui[19]. Both functions are shown in Fig.6B together with the spectrum for quantum flux of daylight[6] and the spectrum of the red patch. As described on page 7 the optical stimulation (quantum catch Q) of a receptor is the integral of the product of spectra for daylight, reflectance, and sensitivity. Bargraphs of Q, normalized to 100% for an ideal flat-white reflectance, are shown in Fig. 6C for white, brown, and red patches. Because there is so little overlap between the red-patch spectrum and the R530 spectrum, the integral is only 6% compared to 29% for R610 of Anartia. The contrast of the red patch against the brown background is only 9% for Vanessa compared to 57% for Anartia. Therefore, the effect of evolutionary adaptation's shifting from the ancestral R530 receptor to the specialized R610 receptor is a dramatic increase in visibility of the red wing patches.

Figure 6D shows examples of reflectance spectra of orange, yellow and white wing patches from the Monarch and Viceroy. The orange and yellow spectra have cutoff-spectra typical of pigmentary colors. The whitish patches of Monarch and Viceroy are spectrally quite different compared to one another.

6. Communication Among Butterflies while Fooling Birds

The importance of red and orange wing patches is a particularly interesting question. The orthodox explanation for the "why" of red/orange wing coloration is to educate vertebrate predators that the butterfly is poisonous if eaten, and thus to reduce predation on members of the mimicry complex[29]. It is not at all necessary for butterflies to be able to see the red/orange patches for mimicry to work. Little attention has been paid, therefore, to the question of visibility of wing markings to members of the mimicry complex. Are there significant differences in wing-reflectance spectra between mimic and model, and are the differences large enough to have value as a signal for species recognition?

Butterflies of the Florida Queen / Florida Viceroy mimicry complex look very similar to avian predators and to us, but not to each other. Queens have receptors peaking at about 360nm, 470nm, and 550nm. Viceroys, on the other hand, have receptors peaking at about 350nm, 450nm, and 515nm (Fig. 4). Thus, Viceroys are much less sensitive at long wavelengths than Queens. The same statement is true for the celebrated Monarch/Viceroy mimicry complex (data not shown).

Reflectance spectra for orange and white patches of Florida Queen and Viceroy are shown in Fig. 7A. The spectra for the orange patches of the two species are very similar, as expected. The spectra for white patches of the two species are quite different at short wavelengths.

Calculated quantum catches (Figs. 7B-C) show very similar stimulation of L- and M-receptors for the Viceroy viewing either orange patch, and for the Queen viewing either orange patch. The UV-sensitive S-receptor is stimulated more strongly by the Viceroy orange, probably because of some UV-reflective scales found on the Viceroy wing but not on the Queen wing.

Comparison of quantum catches for white patches show substantial differences for eyes of both species. All three receptor types have about the same stimulation when viewing Viceroy-white. When viewing Queen-white the stimulation of S-receptors is 40% lower, and the stimulation of M-receptors is about 17% lower than for Viceroy-white. Conclusion: these whitish spots may be important visual signals for species discrimination at long range.

This is curious, for it is now known that most bird eyes contain UV-sensitive photoreceptors[9]. So birds have the capability for detecting the short-wavelength differences in whitish patches, but apparently ignore that data; Behavioral experiments[29] show that birds recognize the similarity in orange coloration of the dorsal wing surfaces and, having regurgitated a Monarch or Queen, are not willing to take a chance on a Viceroy. This, despite the fact that the bird had eaten many Viceroys before experiencing a Monarch or Queen.

7. A New Optical Principle for Camouflage of Beetles

A collaboration with Dr. T.D. Schultz of Arizona State University, to understand the optics of beetle coloration, has

revealed an interesting new mechanism[30] for matching the reflectance spectrum of an insect's body to that of a background. The cuticle is sculptured with hexagonally packed, deep pits ~ 10 microns diameter, that are coated with an 18-layer interference filter. The reflectance spectrum has substantial global variation over a 50 micron patch of surface (eg, a group of 9 bright green pits surrounded by magenta pits). Because these dimensions are well below the resolution limit of animal eyes, a predator sees a spectrum that is an average of the spatially inhomogeneous reflectance spectra, with peak intensity that is controlled by the depth of surface sculpturing. By varying layer thicknesses and sculpturing, different morphs of tiger beetle match the different soils on which they occur, such as wet brown sand, reddish Tertiary sands, or grey basalt pebbles.

8. Visual Attraction of Insects by UV-Reflecting Webs

A collaboration with Prof. C.L. Craig of the Yale Dept. of Biology, to understand the optics of spider silks, has produced a breakthrough in the field of spider ecology & evolution. We learned that some spiders spin silk that selectively reflects ultraviolet light. Spiders use this silk to visually attract insects. One type of UV-reflecting web is found in vegetation gaps illuminated by sunlight and skylight. Redirection of UV light by the web highlights the gap and draws insects to it as they fly from the interior of the vegetation towards open space. Another type of web is decorated with UV-reflecting bars, crosses, discs and bands that attract insects as they search for food resources.

E. LIST OF ALL PUBLICATIONS

G.D. Bernard: Butterfly color vision - spectral properties of photoreceptors and wing patterns. J. Opt. Soc. Am. Series 2, Vol. 3, p44, (1986).

G.D. Bernard: Spectral characterization of butterfly L-receptors using extended Dartnall/MacNichol template functions. J. Opt. Soc. Am. Series 2, 4(13), p123, (1987).

G.D. Bernard, J.K. Douglass and T.H. Goldsmith: Far-Red sensitive visual pigment of a metalmark butterfly. Investigative Ophthalmology 29 Suppl., p350, (1988).

T.D. Schultz and G.D. Bernard: Pointillistic mixing of interference colours in cryptic tiger beetles. Nature 337, 72-73, (1989).

F. LIST OF ALL PARTICIPATING SCIENTIFIC PERSONNEL

Gary D. Bernard

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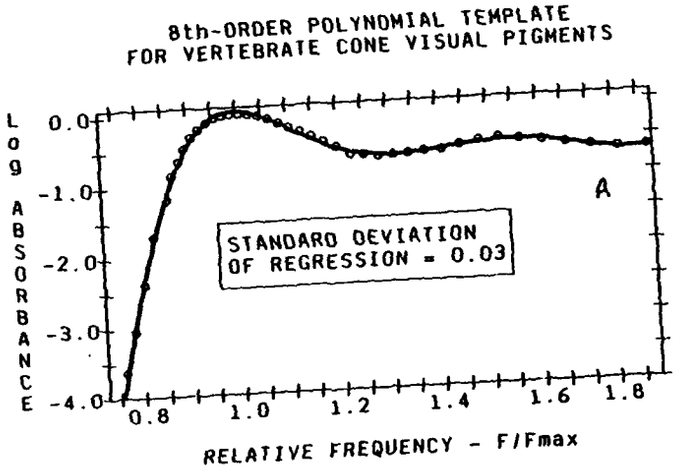
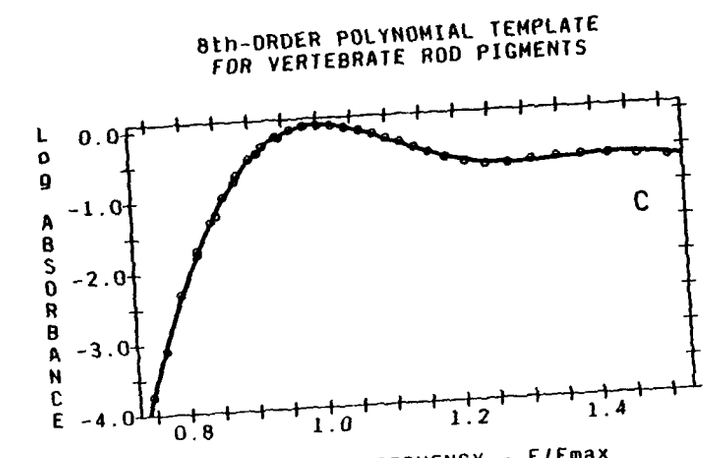
Figure 1: Eighth-Order polynomial templates for vertebrate rod and cone visual pigments.




```
/*      TEMPLATE FUNCTION FOR ABSORPTION SPECTRA      */
/*         OF VERTEBRATE CONE VISUAL PIGMENTS         */
/*      This procedure returns normalized absorbance  */
/*      as a function of wavelength and lambda-max    */

PROCEDURE(wl,wlmax);
F = wlmax / wl;
IF F < 1.831 THEN

z=145.406124*F**8 -1727.740895*F**7 +8798.059416*F**6
                  -25016.668727*F**5 +43311.227824*F**4
                   -46569.815367*F**3 +30212.81385*F**2
                  -10735.353732*F +1582.111534 - 0.040027;
ELSE z=-.730711;
       IF F < .58 THEN z=-8;
RETURN 10**z;
END;
```




```
/*      TEMPLATE FUNCTION FOR ABSORPTION SPECTRA      */
/*            OF VERTEBRATE RHODOPSINS                */
/*      This procedure returns normalized absorbance  */
/*      as a function of wavelength and lambda-max    */

PROCEDURE(wl,wlmax);
F = wlmax / wl;
IF F < 1.53 THEN

z=-797.066398*F**8 +7528.856438*F**7 -30502.839774*F**6
                   +69153.561547*F**5 -95905.820012*F**4
                   +83384.877202*F**3 -44536.370139*F**2
                   +13465.153342*F -1790.343301 -0.008905;

ELSE z=-0.666;
IF F < .58 THEN z=-8;
RETURN 10**z;
END;
```

Figure 2: Absorbance spectra of L-receptor visual pigments.

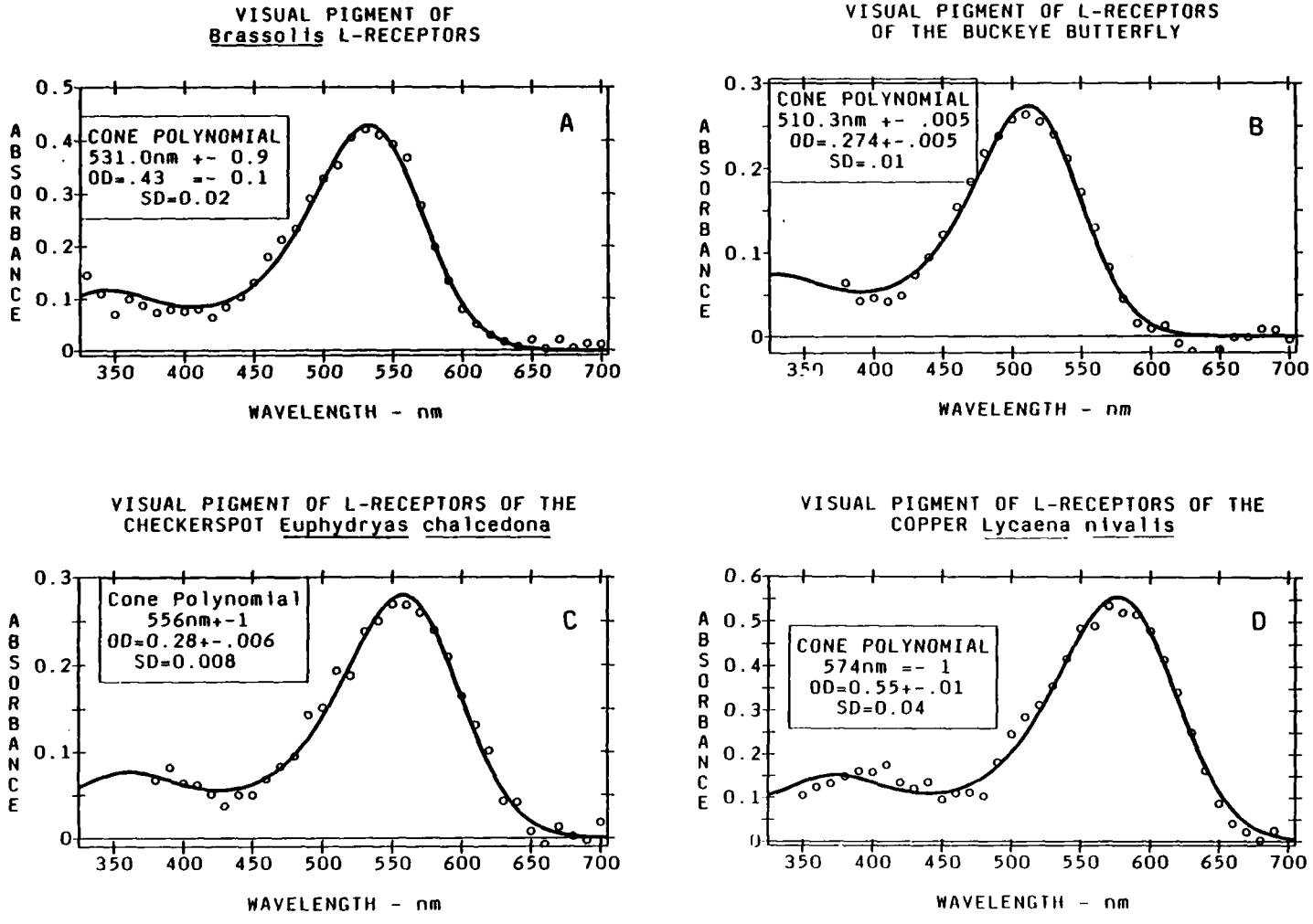


Figure 3: Spectral sensitivity functions for L-receptors.

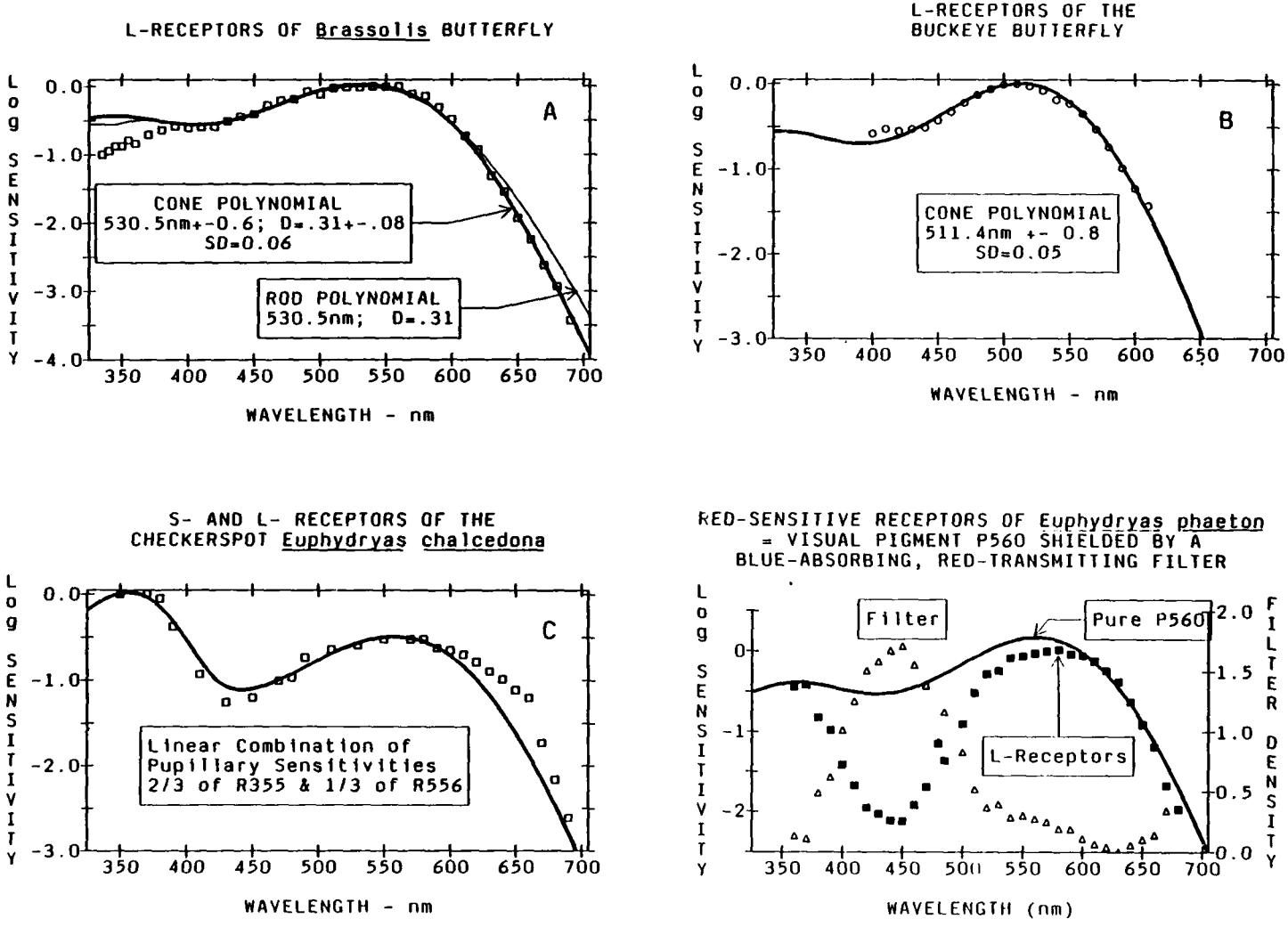


Figure 4: Spectral sensitivity functions for M-receptors.

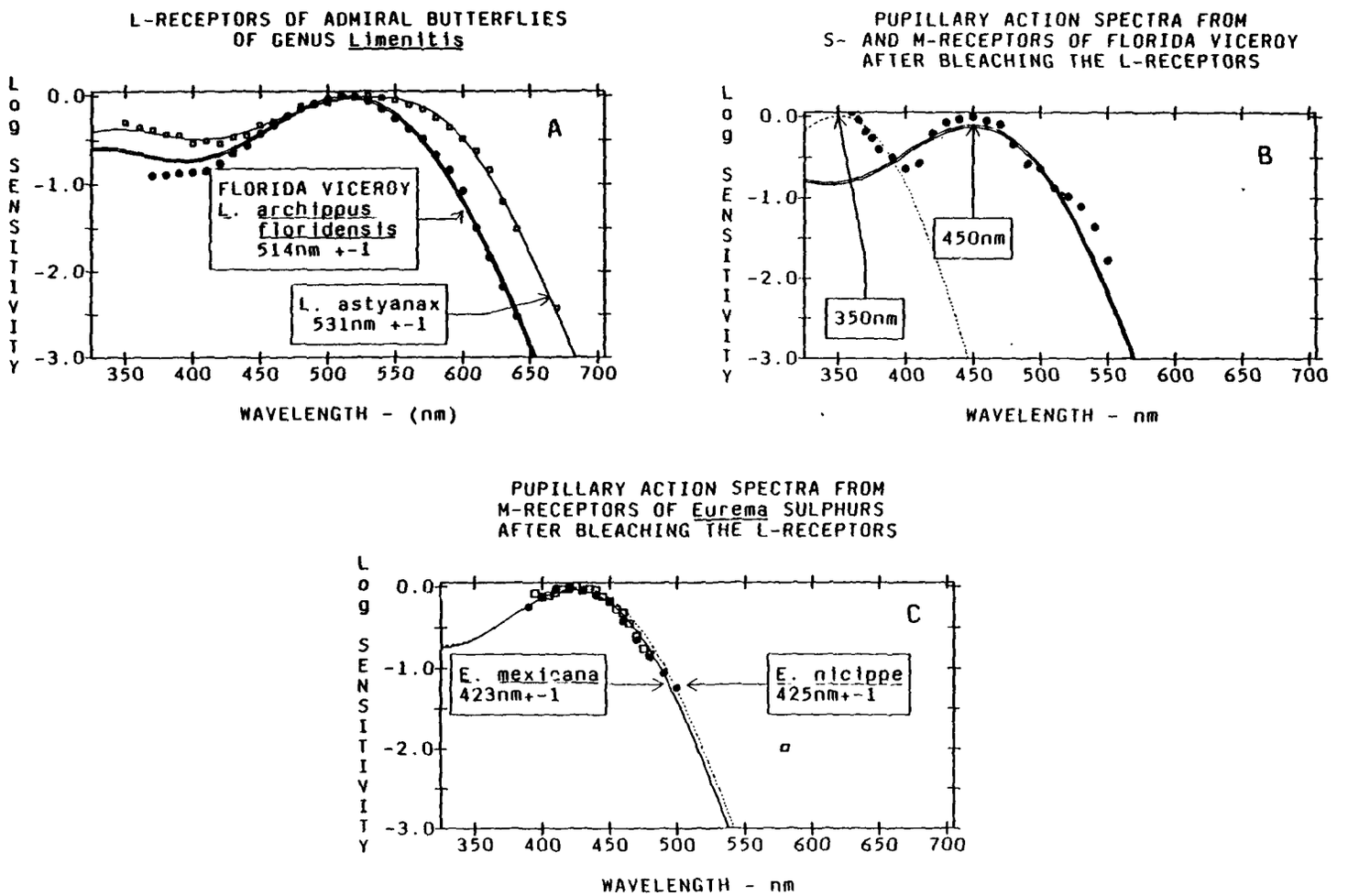


Figure 5: Tetrachromatic eye of Apodemia mormo, and its far-red sensitive visual pigment P600.

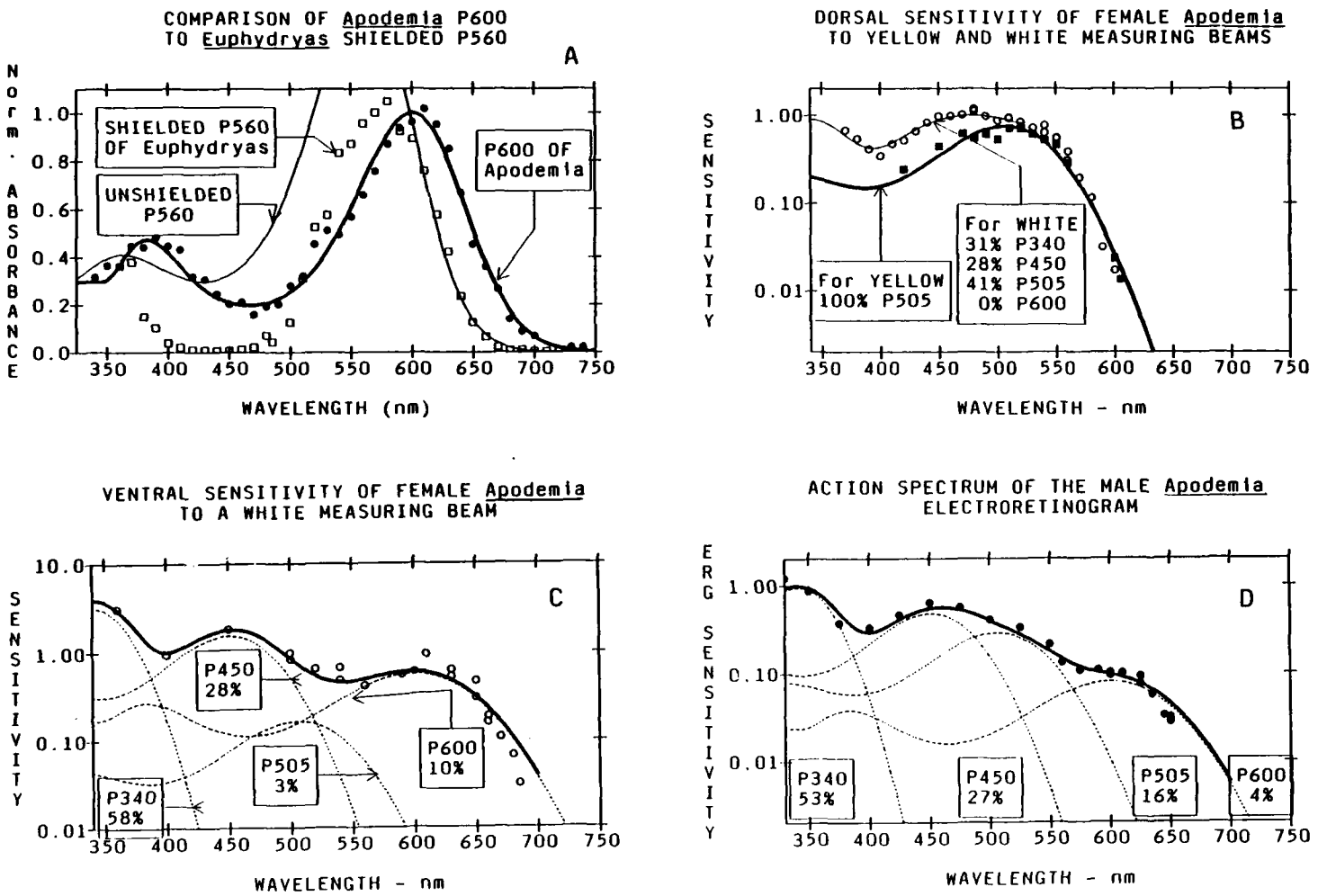


Figure 6: Visibility of colored wing patches.

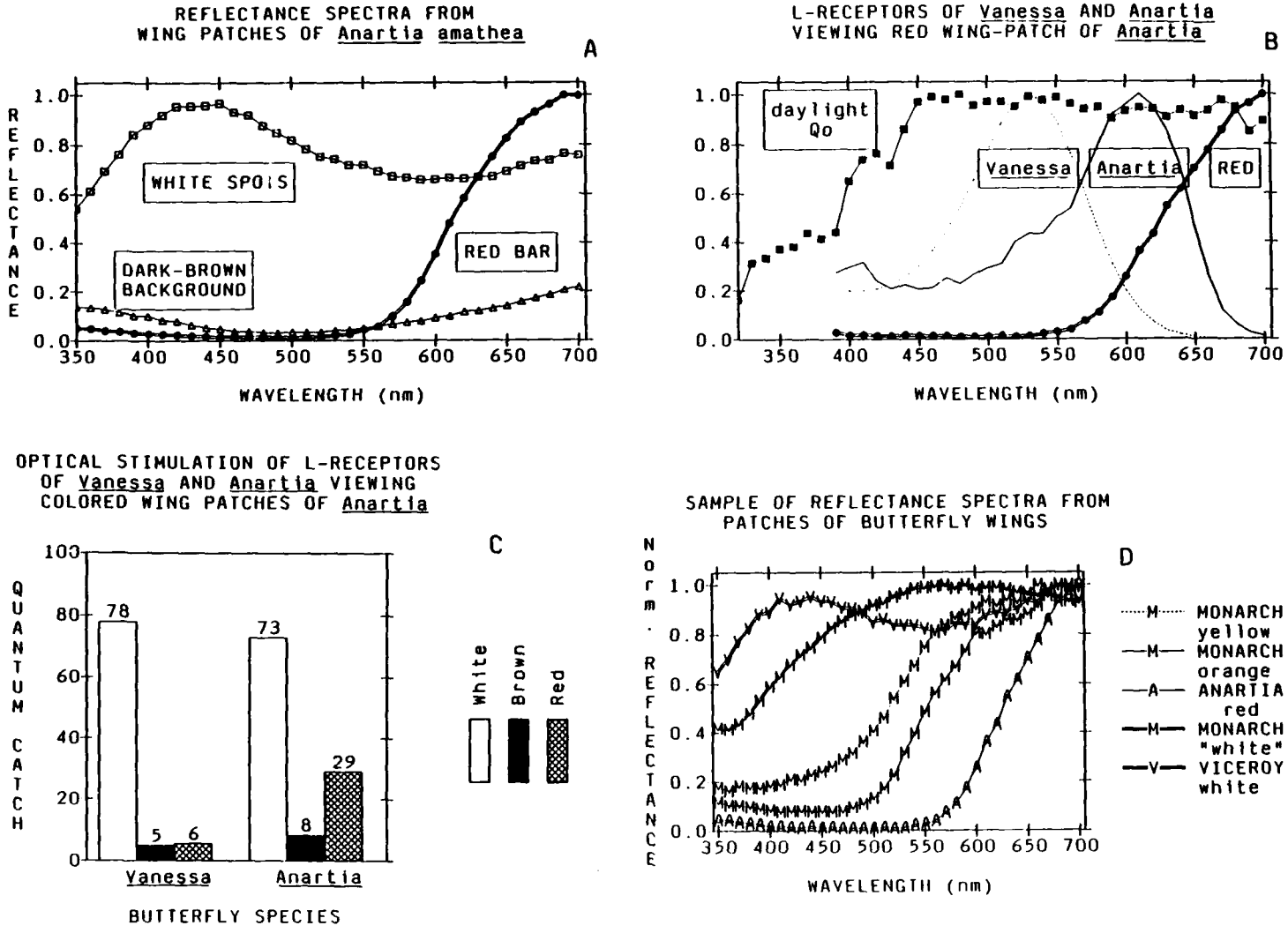


Figure 7: Signal value of white wing markings within a mimicry complex.